tional Corporation, San Diego, CA, 1985), pp. 25–39.
26. T. Poggio *et al.*, in *Proceedings: Image Understanding Workshop*, Cambridge, April 1988 (Morgan Kaufmann, San Mateo, CA, 1988), pp. 1–12.
27. T. A. Cass, in *ibid.*, pp. 640–650.
28. We have exploited the labeling of discontinuities (E. B. Gamble, D. Geiger, T. Poggio, D. Weinshall, in preparation) in recognition experiments. In addition, our integration scheme allows us to segment the scene into different depth planes, for instance, thereby considerably reducing the combinatorics of model-based recognition.
29. Our formulation of the integration problem in terms of MRF does not imply that the algorithms are necessarily stochastic. Deterministic approximations to the more general stochastic schemes may work quite well, especially in situations where redundant and contradictory data from several sources effectively set the initial state of the system close to the solution. We have, in fact, found that gradient descent in the space of the depth and the line process often works quite well. We routinely use a mixed deterministic and stochastic strategy (*17*) in which the continuous (depth) process is deterministically updated while the line process is updated stochastically. Other strategies may also be effective (*8*), such as space-variant filtering, for instance, coupled with edge detection. In addition, time-dependent schedules of the coupling parameters can be useful. They are somewhat similar to simulated annealing, which can also be effectively used, though it is quite slow.
30. H. H. Bülthoff, personal communication.
31. J. F. Canny, *IEEE Trans. Pattern Anal. Mach. Intell.* **PAMI-8** (no. 6), 679 (1986).
32. This report describes research done within the Artificial Intelligence Laboratory. Support for the A. I. Laboratory's artificial intelligence research is provided by the Advanced Research Projects Agency of the Department of Defense under Army contract DACA76-85-C-0010 and in part under Office of Naval Research (ONR) contract N00014-85-K-0124. Support for this research is also provided by a grant from ONR, Engineering Psychology Division, and by a gift from the Artificial Intelligence Center of Hughes Aircraft Corporation to T. Poggio.

4 May 1988; accepted 12 August 1988

Earthquake-Caused Coastal Uplift and Its Effects on Rocky Intertidal Kelp Communities

JUAN CARLOS CASTILLA

The coastal uplift (approximately 40 to 60 centimeters) associated with the Chilean earthquake of 3 March 1985 caused extensive mortality of intertidal organisms at the Estación Costera de Investigaciones Marinas, Las Cruces. The kelp belt of the laminarian *Lessonia nigrescens* was particularly affected. Most of the primary space liberated at the upper border of this belt was invaded by species of barnacles, which showed an opportunistic colonization strategy. Drastic modifications in the environment such as coastal uplift, subsidence, or the effects of the El Niño phenomenon are characteristic of the southern Pacific. Modifications in the marine ecosystem that generate catastrophic and widespread mortalities of intertidal organisms can affect species composition, diversity, or local biogeography.

ON 3 MARCH 1985 AT 19:47 A major earthquake, with a surface wave magnitude of 7.8, occurred in central Chile (*1*). The seismic wave originated in the sea bed 40 km west of the coastal town of Algarrobo (33°20′S, 71°40′W) at a depth of approximately 15 km (*2*). The average horizontal displacements in coastal zones were in a northwest direction and of magnitude approximately 25 cm (*3*). Studies on the vertical component of deformation suggest a mean continental uplift of about 33 cm. Maximum uplifts of approximately 45 to 50 cm were observed in coastal areas, such as El Quisco. The coastal marine station (ECIM) of the Pontificia Universidad Católica de Chile (*4*), located on a 500-m stretch of exposed rocky shore at Las Cruces, is 15 to 20 km from both El Quisco and Algarrobo. The seismic wave caused both horizontal and vertical coastal displacements (*3*) at ECIM. I independently checked rocky shore uplifts at ECIM, using previously known fixed benchmarks that were leveled and referred to the extreme low water spring (ELWS) (*5*). The uplifts (Table 1) found at ECIM, about 44 to 59 cm, were roughly within the range determined by Instituto Geográfico Militar (*3*).

It is well established that the zonation patterns of intertidal organisms are determined by biotic and abiotic factors (*6–8*). Among the latter, desiccation and temperature stress can play key roles determining the upper limit of sessile organisms. Hence, in Chile, even under normal weather conditions during ELWS tides at around noontime on sunny days, intertidal macroalgae have been observed to die (bleaching) (*9*). Moreover, substantial modification of intertidal landscapes has been documented (*10, 11*) as a result of increases in seawater temperature. Similarly, coastal uplifts or subsidences resulting from earthquakes or nuclear testing have modified the intertidal zonation patterns or induced mortalities among sessile or mobile species (*12–15*).

Since 1974 the zonation and dynamics of the central Chile rocky intertidal shore have been studied (*16, 17*). Immediately before the March 1985 earthquake I was engaged in an intertidal research program at Las Cruces (*18*). Transects had been made randomly at selected sites, and species composition, primary space, percent coverage, and the change through time in biomass of the macroalga *Lessonia nigrescens* were assessed (*19*). The first two field surveys were conducted on 9 to 10 February and 5 to 8 March 1985. I report here on the effects of the coastal uplift on ECIM rocky shore communities and particularly on the structure and dynamics of the lower rocky shore fringe, the so-called *L. nigrescens* belt (*9, 16, 20*).

Six 1-m-wide transects in the *L. nigrescens* kelp zone, extending 2.5 m from their intertidal upper to lower limit and 3 to 7 m apart, were randomly chosen (*21*). Vertical differences between the lower and upper limits of the belts were 1 to 1.55 m. Each belt, identified by means of poxy putty marks, was divided vertically into five 0.5-m plots (1-m horizontal axis, 0.5-m vertical axis). Plots A (upper limit) to E (lower limit) were sampled 8 to 11 times during the 36-month study. The maximum holdfast diameter (*d*) of each *L. nigrescens* plant within each plot was recorded and the biomass was calculated (*22*).

Figure 1 shows the change in the *L. nigrescens* biomass with time. In the upper plots, A and B, the biomass before the earthquake was about 15 kg m^{-2}, wet weight; this was considered the normal pattern (*23*). A significant decrease in biomass, accompanied by a change in the color of the plants from brown to yellow and the subsequent mortality of the stipes and holdfasts, was evident toward the end of 1985. By February–March 1986 all plants had disappeared from the upper plots. No recolonization has been observed up to February 1988. The biomass record for the middle plot, C, was similar, but the biomass decrease was obvious only in early 1986. By February 1987 almost all plants had disappeared from this plot as well, and no recolonization has since been observed. Plots D and E, the lower plots, behaved differently. At plot D a drastic decrease in *L. nigrescens* biomass was observed in early 1986 (*23*) (about 6 kg m^{-2} by February 1987), but by February 1988 the biomass had increased to about 15 kg m^{-2}. Plot E showed comparatively less change in *L. nigrescens* biomass, with values between 20 and 33 kg m^{-2}. In plot F (not part of the original study because the kelp was absent) *L. nigrescens* was abun-

---

Estación Costera de Investigaciones Marinas, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

dant by the beginning of 1986 owing to the settlement of juvenile plants; this observation suggests a change in the lower intertidal limits of the kelp belt, as compared with the original study. By February 1987 *L. nigrescens* biomass in plot F was about 15 kg m^{-2}, and by February 1988 it had reached 30 kg m^{-2}.

Changes in primary space cover over time were determined at three levels in the *L. nigrescens* belt (Fig. 2): (i) upper level (plots A and B), (ii) middle level (plots C and D), and (iii) lower level (plot E). At the upper level there was evidence of the mortality of *L. nigrescens* and of the presence of articulate and crustose coralline algae a few months after the earthquake. By February 1986 the cover of the algae was almost zero. As primary space became available, it was immediately occupied by barnacles, mostly *Chthamalus scabrosus* and to a lesser extent *Jehlius cirratus*, which readily settled on these plots and thereafter established a belt (*24*). The cover of barnacles increased from 18 to 66% in the 3 years after the earthquake (*25*). At the middle level a similar process occurred. Bleaching of macroalgae was observed later. For example, the cover of crustose coralline algae diminished from about 30% in March 1985 to about 10% in February 1988. *Chthamalus scabrosus* increased its cover in these plots from less than 5% in March 1985 to 56% in February 1988. At the lower level (only plot E was studied because of the inaccessibility of plot F) few changes were observed. The primary space cover of *L. nigrescens* increased from about 20 to 45%. No barnacles settled at this plot in amounts exceeding 5%, and therefore they are included under the "other species" category in Fig. 2. A decrease in the cover of crustose and articulate coralline algae was also observed at this plot. No settlement of the competitively dominant intertidal mussel *Perumytilus purpuratus* has been observed to date.

In Alaska, Plafker (*26*) used intertidal barnacles to determine changes in the elevation of coastal areas due to the great earthquake of 27 March 1964. Studies on laminarian and coralline algae after the earthquake (*27*) demonstrated dramatic changes in zonation patterns and in the relative ability of those organisms to survive under conditions of coastal uplift. Most coralline algae require nearly continuous submergence, and coastal uplift is bound to affect their populations and eventually the community.

Similar sudden and dramatic ecologically catastrophic events attributed to El Niño phenomena (*11*) have substantially modified intertidal landscapes. Hence, extensive mortalities of adult *L. nigrescens*, resulting in the

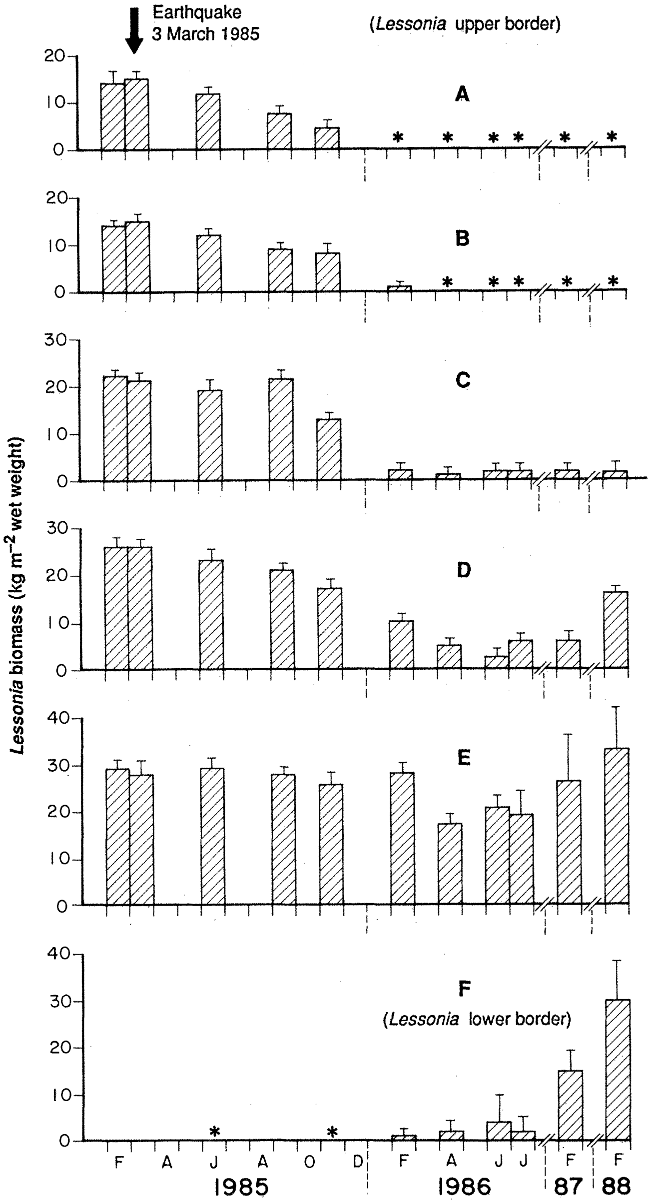


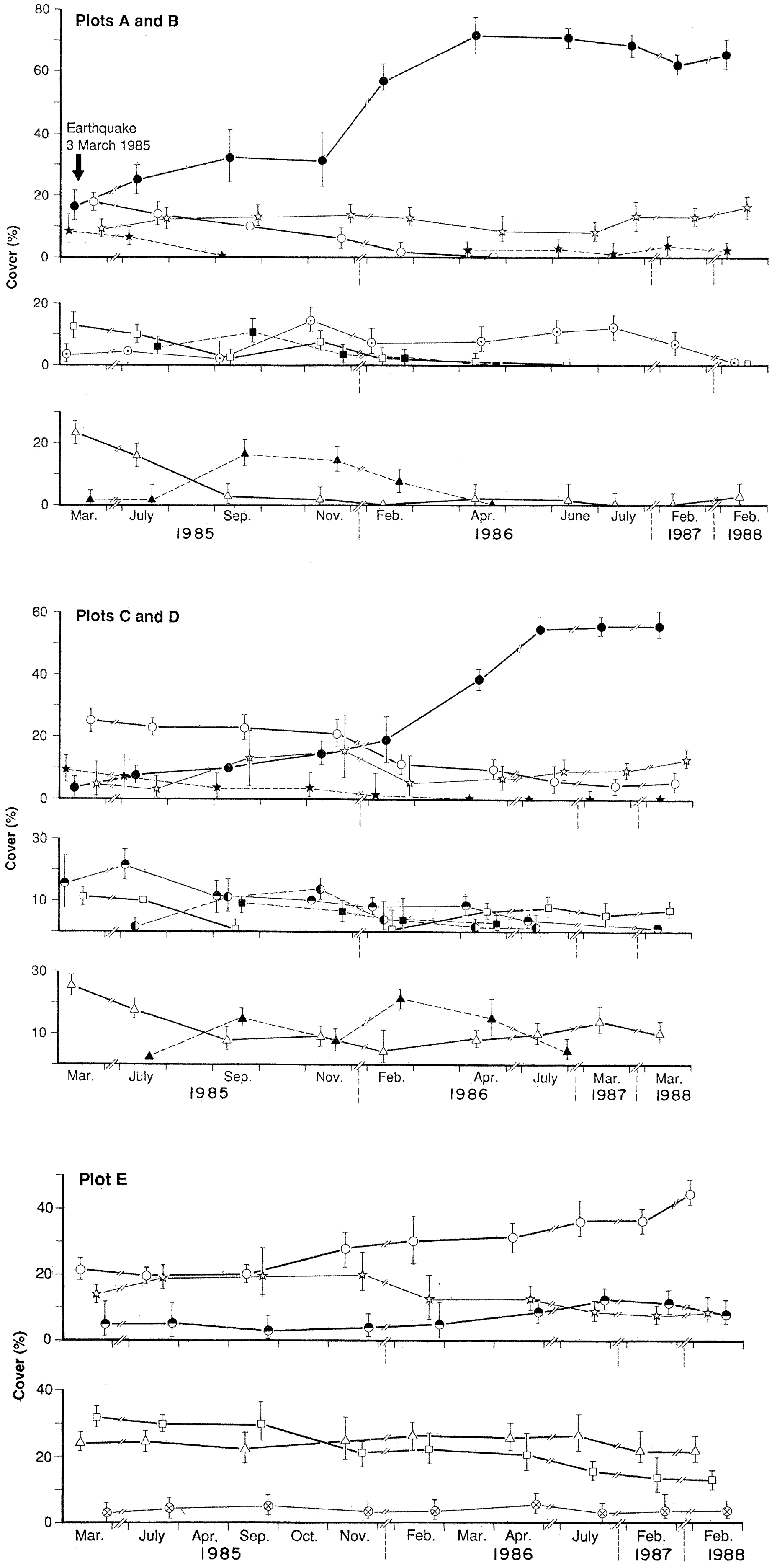
Fig. 1. *Lessonia nigrescens* biomass change along time in different intertidal plots (A = upper *Lessonia* border; F = lower border). Biomass and standard errors (bars) are based on six readings per plot. Asterisks indicate observations with zero biomass.

Table 1. Coastal vertical movement of rocks at ECIM (Las Cruces) associated with the 3 March 1985 earthquake. Each set of readings was taken at the same location between 5 and 20 min before the calculated tide table low tide of the corresponding day (*5*).

Date	Relative height (cm) referred to ELWS: Mean	(SD)	Approximate uplift (cm)
	Wall 1		
Before earthquake			
20 August 1982	65.3	(4.1)*	
1 December 1982			
6 October 1982			
After earthquake			
3 June 1985	109.9	(5.3)†	+44.6
4 June 1985			
	Wall 2		
Before earthquake			
6 October 1983	172	(3.9)*	
After earthquake			
3 June 1985			
4 June 1985	231	(7.2)†	+59.0

*Data from twelve readings taken by two operators. †Data from eight readings taken by four operators.

Fig. 2. Changes in primary space cover along time at three levels of the *Lessonia nigrescens* intertidal belt: plots A and B, upper; C and D, middle; and E, lower; ●, Barnacles; ○, *Lessonia nigrescens*; ★, bare space; ☆, other species; □, *Corallina* spp. alive; ■, *Corallina* spp. dead; △, lithothamnioid alive; ▲, lithothamnioid dead; ⊙, *Hildenbrandia* sp.; ◓, *Codium dimorphum* alive; ◐, *Codium dimorphum* dead; ⊗, *Gelidum chilense.* Averages and standard errors (bars) are based on six readings per plot.



depopulation of large areas of rocky shores in northern Chile, are well documented (*10*).

Both kinds of catastrophic events, earthquakes and El Niño phenomena, are cyclical and affect large areas of the Chilean coastline. For instance, seven earthquakes of surface wave magnitude greater than 7 occurred in central Chile in the last century (*1*). Further, it has been calculated that the recurrence time for earthquakes of magnitude greater than 8.2 to 8.4 is about 86 ± 10 years (*1*). An El Niño (*28*) occurs on average every 4 years, with intervals between successive events as short as 2 years and as long as 10 years (*29*).

These kinds of sudden and drastic modifications in the environment, which are characteristic of the southeastern Pacific, can cause substantial changes in marine ecosystems and can generate catastrophic mortalities that can affect local biogeography, species composition and diversity, and biomass; they can enhance local and more widespread latitudinal patchiness [much the same as mortalities produced by disease outbreaks (*30–32*) or predation (*33*)]. Examples of the historical and ecological importance of drastic and catastrophic events and their effects on marine communities have been reported (*34, 35*) for the Northern Hemisphere. The question of whether some of the rocky intertidal species have evolved in response to these cyclical catastrophic events is particularly challenging. Recently (*36*) it was demonstrated that marine organisms respond rapidly to intense perturbations (predation) within ecological time frames.

REFERENCES AND NOTES

1. L. Ponce, S. K. Singh, G. Suarez, J. Vargas, *Inf. Téc. SC/RP 203121.5* (Centro Regional de Sismología para América del Sur, Lima, Perú, 1985), p. 1.
2. The tectonic plates in motion are Nazca and South America. The speed of the seismic wave caused by the March 1985 earthquake was about 5 km sec^{-1}.
3. Departamento de Procesamiento y Cálculo, Instituto Geográfico Militar, *Terra Aust.* **29**, 5 (1986).
4. Estación Costera de Investigaciones Marinas (ECIM), Las Cruces, in operation since December 1982.
5. Two benchmarks identified on rocks of ECIM, one next to the seawater intake at the south end of the station and another in the northern border, were used to independently check on rock upliftings. Tides in this coastal line are of the mixed diurnal-

semidiurnal type with greatest amplitude of about 1.80 m.
6. J. R. Lewis, *The Ecology of Rocky Shores* (English Univ. Press, London, 1964).
7. J. Connell, *Annu. Rev. Ecol. Syst.* **3**, 169 (1972).
8. R. T. Paine, in *Changing Scenes in Natural Science*, C. E. Goulden, Ed. (Special Publication 12, Academy of Natural Sciences, Philadelphia, 1977), pp. 245–270.
9. B. Santelices, S. Montalva, P. Oliger, *Mar. Ecol. Prog. Ser.* **6**, 267 (1981).
10. R. Soto, *Invest. Pesq. (Chile)* **32**, 199 (1985).
11. R. T. Paine, *Estud. Oceanol.* **5**, 9 (1986).
12. C. Darwin, *Geological Observations* (Appleton, New York, 1897).
13. *The Great Alaska Earthquake of 1964* (National Academy of Sciences, Washington, DC, 1971).
14. P. Bodin and T. Klinger, *Science* **233**, 1071 (1986).
15. P. A. Lebendik, *Mar. Biol.* **20**, 197 (1973).
16. J. C. Castilla, *Medio Ambiente* **5**, 190 (1981).
17. R. T. Paine *et al.*, *Am. Nat.* **125**, 679 (1985).
18. The research program was designed to evaluate the ecological role played by man as a predator on the rocky shore of central Chile. Castilla and Durán (*33*) and D. Oliva and J. C. Castilla [*Publ. Stazione Zool. Napoli I Mar. Ecol.* **7**, 201 (1986)] discuss the aims of the program.
19. The point-intercept method was used: a 1 m by 1 m string-grid quadrat with 171 intersection points was applied to the surface. Percent coverage was calculated by angular transformation.
20. E. P. Guiler, *Pap. Proc. R. Soc. Tasmania* **93**, 165 (1959).
21. All *L. nigrescens* belts selected were in rocks with inclinations of 45° or less and presented a similar geological composition consisting primarily of metamorphic gneiss with lamprophyre intrusives. They were oriented south and received water splash through littoral channels.
22. I calculated the *L. nigrescens* biomass (b), wet weight, for three types of plants according to the following formulas: (i) for undamaged plants, $b = 0.7208\ d$ (where d is the maximum diameter of holdfast); (ii) for half-damaged plants (less than 50% of the stipes dead), $b = 0.5593\ d$; and (iii) for fully damaged plants (more than 50% of the stipes dead), $b = 0.2035\ d$.
23. *Lessonia nigrescens* biomass determinations carried out on six different opportunities (1982 to 1984) at Las Cruces showed values ranging between 13 to 20 kg m^{-2}, wet weight, at the upper intertidal border and 27 to 38 kg m^{-2} at the middle and lower borders. The mean overall biomass of this kelp at Los Molles, central Chile, was about 33 kg m^{-2} [B. Santelices, "Manejo de praderas de *Lessonia nigrescens* en Chile Central" (final report, Subsecretaria de Pesca, Chile, 1981)].
24. Newly settled *J. cirratus* and *C. scabrosus* are difficult to identify in the field. After 3 to 5 months, about 90% of the barnacles at this level were *C. scabrosus*, and they reached 100% by the end of the study.
25. R. T. Paine [*Paleobiology* **7**, 553 (1981)] argued that in Chilean rocky shores both species of barnacles showed a "weed" colonization strategy.
26. G. Plafker, *Science* **148**, 1675 (1965).
27. H. W. Johansen, in (*13*), pp. 35–68.
28. M. A. Cane, *Science* **222**, 1189 (1983).
29. W. H. Quinn *et al.*, *Fish. Res. Bull.* **76**, 663 (1978).
30. M. L. Dungan *et al.*, *Science* **216**, 989 (1982).
31. H. A. Lessios *et al.*, *ibid.* **226**, 335 (1984).
32. T. P. Hughes *et al.*, *Bull. Mar. Sci.* **36**, 377 (1985).
33. J. C. Castilla and R. Durán, *Oikos* **45**, 391 (1985).
34. P. K. Dayton and M. J. Tegner, *Science* **224**, 283 (1984).
35. D. S. Wethey, *Ecology* **66**, 445 (1985).
36. R. H. Seeley, *Proc. Natl. Acad. Sci. U.S.A.* **83**, 6897 (1986).
37. Supported by projects Dirección de Investigación Universidad Católica 63/84 and Fondo Nacional de Investigación Científica y Tecnológica 86/1100. I thank D. Oliva, E. Ortiz, R. Bustamante, and R. Durán for field assistance and helpful discussions. Two anonymous referees made valuable comments on the manuscript.

18 April 1988; accepted 21 July 1988

Activation of Muscarinic Potassium Currents by ATPγS in Atrial Cells

ANGELA S. OTERO,* GERDA E. BREITWIESER, GABOR SZABO

Intracellular perfusion of atrial myocytes with adenosine 5′-(γ-thio) triphosphate (ATPγS), an ATP analog, elicits a progressive increase of the muscarinic potassium channel current, $I_{K(M)}$, in the absence of agonists. In this respect, ATPγS mimics the actions of guanosine triphosphate (GTP) analogs, which produce direct, persistent activation of the guanyl nucleotide–binding (G) protein controlling the $K^{+}_{(M)}$ channel. The effect of ATPγS on $I_{K(M)}$, however, differs from that produced by GTP analogs in two aspects: it requires relatively large ATPγS concentrations, and it appears after a considerable delay, suggesting a rate-limiting step not present in similar experiments performed with guanosine 5′-(γ-thio) triphosphate (GTPγS). Incubation of atrial homogenates with [^{35}S]ATPγS leads to formation of significant amounts of [^{35}S]GTPγS, suggesting that activation of $I_{K(M)}$ by ATPγS arises indirectly through its conversion into GTPγS by cellular enzymes. ATPγS is often used to demonstrate the involvement of protein phosphorylation in the control of various cellular processes. The finding that cytosolic application of ATPγS can also lead to G-protein activation implies that experiments with ATPγS must be interpreted with caution.

INTERNAL DIALYSIS OF ATRIAL MYOCYTES with hydrolysis-resistant GTP analogs evokes muscarinic receptor–independent activation of $I_{K(M)}$ (*1*, *2*) with an order of effectiveness (GTPγS > GMP-PNP ≃ GTP > GMP-PCP; where GMP-PNP is guanylyl imidodiphosphate and GMP-PCP is guanylyl (β,γ-methylene)-diphosphonate) that parallels their binding affinities to purified G proteins (*3*, *4*). We found (*5*) that intracellular application of ATPγS, an ATP analog, has effects that closely resemble those of GTP analogs (*1*, *6*) on $I_{K(M)}$. This result could be interpreted as a lack of specificity of the nucleotide site involved in muscarinic activation of cardiac K^+ channels, thus weakening the G-protein transduction hypothesis, since ATP interacts poorly, or not at all, with the GTP binding site of purified G proteins (*7*). Alternatively, the actions of ATPγS could stem from (i) contamination by GTPγS, (ii) formation of a stable thiophosphorylated protein involved in channel gating, or (iii) conversion of ATPγS into its guanosine counterpart. The experiments reported here were designed to distinguish among these possibilities.

The effects of intracellular application of ATPγS on K^+ currents were examined in single myocytes dissociated enzymatically from bullfrog atrium, with the tight-seal whole-cell voltage clamp technique (*1*, *8*). Calcium and Na^+ currents were blocked by extracellular cadmium and tetrodotoxin, respectively. Outward and inward currents were measured at the end of 250-ms pulses from a holding potential of −85 to −45 mV and −135 mV, respectively. Figure 1A shows these values, plotted as a function of time, beginning 1 min after the disruption of the patch membrane; the patch pipette solution contained 2.5 m*M* ATPγS. A gradual increase in both inward and outward current is observed after 7 min of dialysis. Superfusion of the cell with 1 μ*M* acetylcholine (ACh) 10 min after patch rupture causes a rapid, albeit small, increase in current; washout of agonist 1 min later has little effect on the current levels, indicating persistent activation of $I_{K(M)}$. The membrane currents elicited by the test pulses are shown in Fig. 1B, which illustrates the appearance of the characteristic relaxation of $I_{K(M)}$ (*1*, *9*) well before agonist was applied. The current-voltage (*I-V*) relations measured at various times during this experiment are plotted in Fig. 1C. It is clear that the voltage dependence of the current activated by ATPγS differs from that of the background K^+ channel, I_{K1}, and parallels that observed during ACh application. External application of 0.1 m*M* $BaCl_2$, but not 1 μ*M* atropine, completely blocks the membrane currents elicited by ATPγS. By these criteria, the current that develops during intracellular perfusion with ATPγS is indistinguishable from $I_{K(M)}$, whether elicited by agonist application or by intracellular dialysis with GTP analogs (*1*).

We examined the effect of loading cells with different ATPγS concentrations in experiments similar to that in Fig. 1. After receptor-independent activation had reached a steady level, 1 μ*M* ACh was added

---

A. S. Otero and G. Szabo, Department of Physiology and Biophysics, University of Texas Medical Branch, Galveston, TX 77550.
G. E. Breitwieser, Department of Physiology, Johns Hopkins University School of Medicine, Baltimore, MD 21205.

*To whom correspondence should be sent.